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Ophiotaenia lapata sp. n. (Eucestoda: Proteocephalidea) from Madagascar: a parasite of the endemic snake *Madagascarophis colubrinus* (Colubridae)

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Abstract: *Ophiotaenia lapata* sp. n. (Cestoda: Proteocephalidea) from Madagascar: a parasite of the endemic snake *Madagascarophis colubrinus* (Colubridae). - A new proteocephalidean cestode, *Ophiotaenia lapata* sp. n., is described from the gut of the endemic colubrid snake *Madagascarophis colubrinus* (Schlegel, 1837) (Colubridae) from Madagascar. The new species differs from all but one *Ophiotaenia* species parasitic in African snakes by the presence of an apical organ. *Ophiotaenia lapata* differs from *O. adiposa* Rudin, 1917, which also possesses an apical organ, by the number of testes (89-170 in the new species versus 170-220 in *O. adiposa*), by the position of the genital pore in relation to the anterior margin (43-53% of proglottis length in *O. lapata* versus 20-25%) and the scolex width (240-280 µm in the former species versus 500-600 µm in the latter). The new species possesses, unlike all but one *Ophiotaenia* species parasitic in African snakes, a three-layered embryophore. The other African species have two-layered embryophore except for *Ophiotaenia georgievi* de Chambrier, Ammann & Scholz, 2010, which can be distinguished by the absence of an apical organ, by the number of uterine branches on each side (23-28 in *O. georgievi* versus 41-68 in *O. lapata*) and by the total length of the strobila (50 mm in *O. georgievi* and 295 mm in *O. lapata*). *Ophiotaenia lapata* is the third proteocephalidean cestode reported from Madagascar.

Keywords: Eucestoda - taxonomy - morphology - Serpentes - helminths - Africa.

INTRODUCTION

Tapeworms of the order Proteocephalidea Mola, 1928 are frequent and cosmopolitan parasites of freshwater fishes, reptiles and amphibians (Rego, 1994). The genus *Ophiotaenia* La Rue, 1911 comprises ninety-six species parasitic in reptiles and amphibians (for a list of species see Schmidt, 1986; de Chambrier *et al.*, 2010, 2012). Two specimens of the colubrid snake *Madagascarophis colubrinus* (Schlegel, 1837)

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endemic to Madagascar were examined in 2011 by the present authors. They harboured proteocephalidean cestodes belonging to *Ophiotaenia*, which are described herein as a new species.

MATERIALS AND METHODS

Snakes examined were killed by injection of Nembutal (sodium pentobarbitone) and immediately dissected. Freshly collected tapeworms were rinsed in a saline solution (0.9% in water), placed in a Petri dish with a small quantity of saline and fixed with hot, almost boiling 4% neutral formalin. After 1-3 weeks, the worms were transferred and stored in 75% ethanol solution. The worms used for morphological study were stained with Mayer's hydrochloric carmine, destained in 75% acidic ethanol (i.e. 75% ethanol with about 2 ml HCl/100 ml), dehydrated in an ethanol series, cleared with eugenol (clove oil) and mounted as permanent preparations in Canada balsam. For histology, pieces of the strobila were embedded in paraffin wax, sectioned transversely at 15 µm intervals, stained with Weigert's haematoxylin and counterstained with 1% eosin B acidic solution (see Scholz & Hanzelova, 1998; de Chambrier, 2001; Oros *et al.*, 2010). Eggs were studied in distilled water. Scolex for scanning electron microscopical (SEM) observation was dehydrated in a graded ethanol series (80%, 96%, twice 100%), then transferred to a graded amyl/acetate series, critical point-dried in CO_2, sputter coated with gold and examined with a Zeiss 940A electron microscope at the Natural History Museum, Geneva. Microthrix terminology follows Chervy (2009).

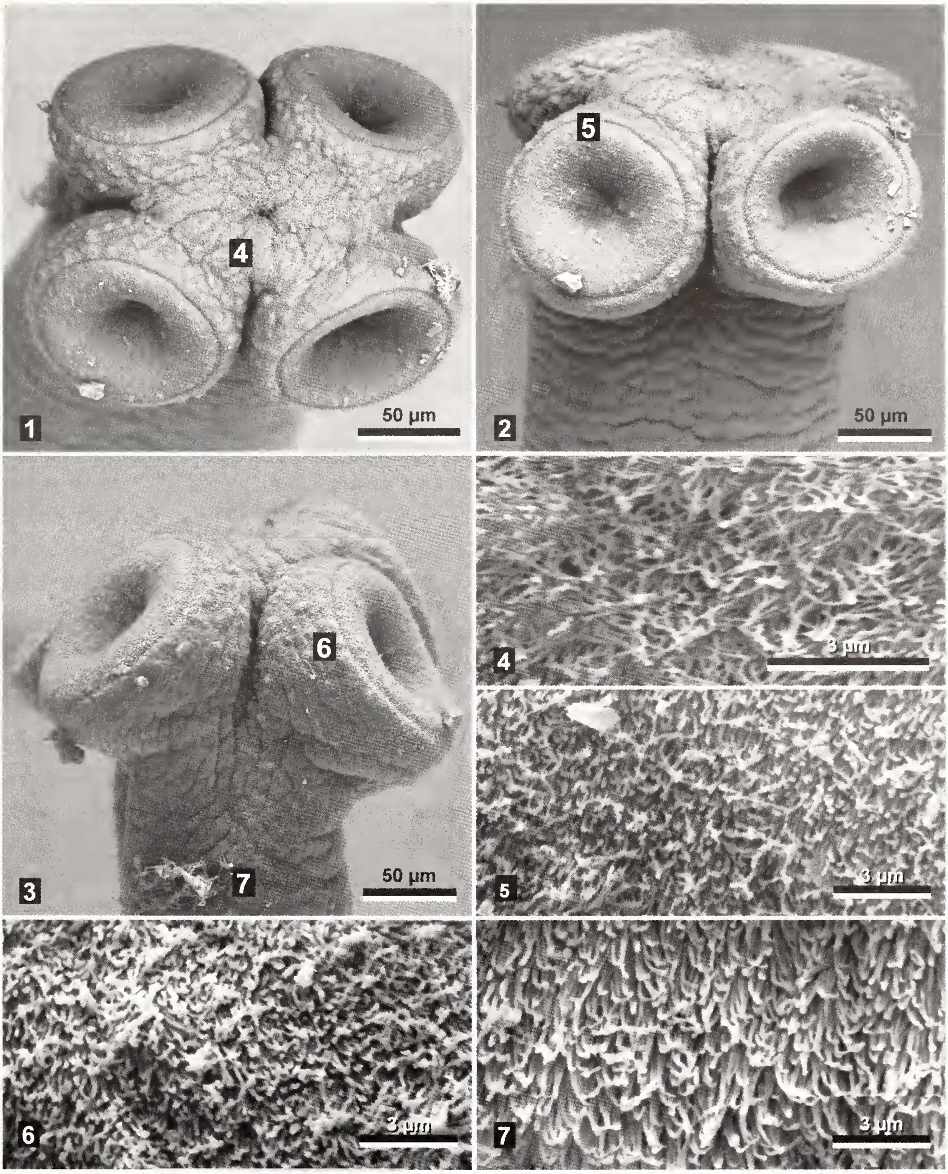
All measurements are given in micrometres unless otherwise indicated. Abbreviations used in the description are as follows: x = mean; n = number of measurements; CV = coefficient of variability (expressed in %); RSO = ratio of the width of the ovary to the width of the proglottis; PGP = position of genital pore (cirrus pore) expressed as percentage of its position to the proglottis length from the anterior margin; RSCS = relative size of the of cirrus-sac expressed as percentage of its length to the width of the proglottis.

The worms studied were compared with those collected by G. Brygoo, Madagascar Pasteur Institute, between 1960 and 1970. His collection of tapeworms from snakes and amphibians from Madagascar was originally deposited in the Institute of Zoology in Neuchâtel, Switzerland, and then transferred to the Natural History Museum in Geneva. New material studied has been deposited in the helminthological collection of the Natural History Museum, Geneva, Switzerland (acronym MHNG PLAT), in the Department of Animal Biology, Faculty of Sciences, University Antananarivo, department of Animal Biology (acronym UADBA), and in the Institute of Parasitology, České Budějovice, Czech Republic (acronym IPCAS).

RESULTS

Ophiotaenia lapata sp. n. Figs 1-14

Type material: Holotype MHNG-PLAT-79567 (field number Mad 007a) (1 slide) and 7 paratypes: MHNG-PLAT-79568 (Mad 007b), 3 whole mounted slides and 18 cross sections; MHNG-PLAT-82165 (Mad 007p), 1 slide; MHNG-PLAT-82166 (Mad 007x), 1 slide, scolex used for SEM; MHNG-PLAT-82167 (Mad 007z), 1 whole mounted slides and 10 transverse sections; MHNG-PLAT-79570 (Mad 008a), 1 whole mounted slide. UADBA No50001 and 50003, (Mad 007), two specimens, 2 slides.



FIGS 1-7

Ophiotaenia lapata sp. n. Scanning electron micrographs. Paratype (MHNG-PLAT-82166, field number Mad 007HFx). (1) Scolex, apical view (2) Scolex, dorsoventral view. (3) Scolex, lateral view. (4) Capilliform filitriches at level of the apex of the scolex. (5) Capilliform filitriches and small gladiate spinitriches at marginal surface of sucker. (6) Capilliform filitriches and small gladiate spinitriches at non-adherent surface of sucker (7) Gladiate spinitriches at proliferation zone surface. Scale-bars: 1-3 = 50 µm; 4-7 = 3 µm.

OTHER MATERIAL: MHNG-PLAT-82172 (field number Mad 007hf), 2 whole mounted slides, (voucher material used for the study of the eggs). – MHNG-PLAT-82169 (field number Mad 007y), 1 whole mounted slides and 10 transverse sections. – UADBA No50002, 50004 (field number Mad 007), and 50005 (field number Mad 007c), 3 mounted slides. Some pieces of gravid proglottides were placed in alcohol for DNA analyses. – MHNG-PLAT-79569 (Mad 007c); MHNG-PLAT-82175 (Mad 008hf), and IPCAS C-625, 1 whole mounted slide and 4 slides of serial cross sections (from MHNG-PLAT-82175). – MHNG-PLAT-73222, from Brygoo material; Madagascar, Befandriana S., October 1967, 1 whole mounted slide and 13 transverse sections.

TYPE LOCALITY: Ambinda Nord/Beanka (-17.93986°Lat; 44.46822°Long), 18 November 2011. All material listed above is from this locality, except MHNG-PLAT-73222.

DESCRIPTION (based on 8 specimens, 4 complete and 4 incomplete): Proteocephalidae, Proteocephalinae.

Cestodes up to 295 mm long; maximum width 1.2 mm. Strobila acraspedote, anapolytic. All proglottides longer than wide (length: width ratio 1.03-1.52 to 4.80-6.00, from immature to gravid). Scolex 120-150 long and 190-280 (n = 3) wide, slightly wider than neck (Figs 1-3, 8). Suckers uniloculate, round, slightly embedded, 85-115 (n = 12) in diameter, representing 30-48% of scolex width (Figs 1, 2). Apical organ 40-45 in diameter, i.e. 15-19% of scolex width, surrounded by cells with finely granular cytoplasm (Fig. 8). Proliferation zone 2.5-3.6 mm long and 140-185 wide.

Internal longitudinal musculature weakly developed, anastomosed, formed by numerous tiny muscle fibres (Figs 10, 11). Ventral osmoregulatory canals overlapping testes, reaching laterally vitelline follicles, 5-25 in diameter, with secondary canals directed externally; dorsal canal narrow, thick-walled, 5-10 in diameter (Fig. 13).

Testes medullary, on one layer, in two narrow lateral bands (poral field separated by terminal genitalia to preporal and postporal groups). Testes rarely reach anterior margin of proglottis, but never reach to ovary, occupying 81-88% of total length of proglottis (Figs 10, 13, 14). Testes 89-170 (x = 128, n = 38, CV = 17%) in number, with 47-84 (x = 66) aporal testes, 25-49 (x = 37) preporal testes and 19-38 (x = 29) postporal testes. Testes spherical, 50-65 (x = 55, n = 22) in diameter, degenerated in gravid proglottides (Fig. 14).

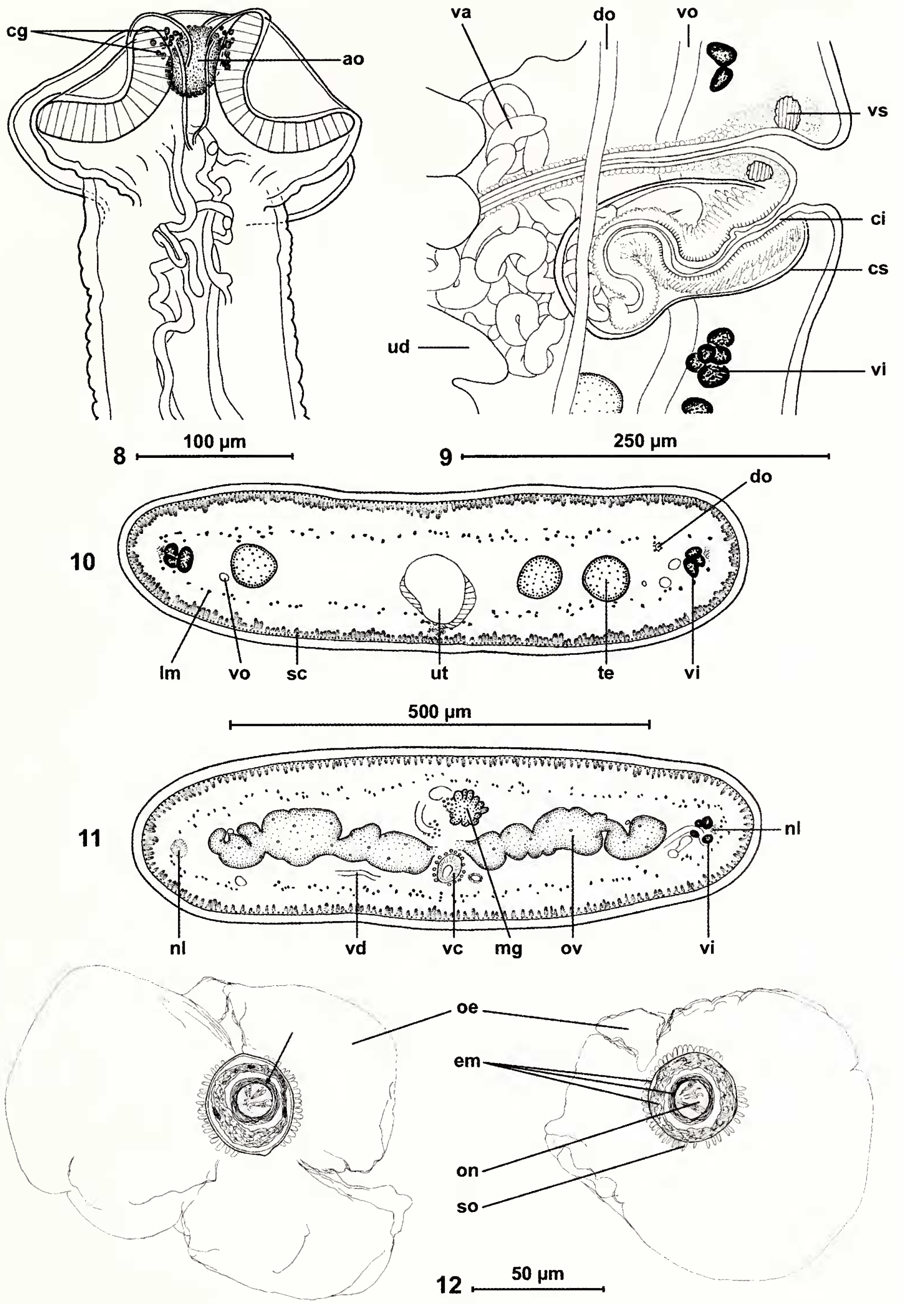
Cirrus-sac elongate, thick-walled, 170-250 (x = 210, n = 53) long and 75-90 (x = 80 , n = 10) wide (Fig. 9); RSCS 19-26 % (x = 22%, n = 53, CV = 8 %). Cirrus length represents about 70% of cirrus-sac length. Vas deferens strongly coiled, situated between proximal part of cirrus-sac and midline of proglottides, but never crossing it.

Genital atrium present; genital pores alternating irregularly, more or less equatorial, PGP = 43-53% (x = 49 %, n = 12, CV = 6%) (Figs 13, 14). Genital ducts passing between osmoregulatory canals.

Ovary medullary, bilobed (Figs 11, 13, 14), 520-840 wide, RSO = 68-81% (x = 75%; n = 55; CV = 4%). Mehlis' glands 50-80 (x = 60, n = 9) in diameter, representing 9-12% of proglottis width (Figs 11, 13, 14).

FIGS 8-12

Ophiotaenia lapata sp. n. (8) *Holotype*, scolex, dorsoventral view (MHNG-PLAT-79567). (9) Paratype, vagina and cirrus-sac region, dorsal view (MHNG-PLAT-79568). (10-11) Transverse sections of a mature proglottis at level of anterior part and ovary, respectively (MHNG-PLAT-82167). (12) Eggs drawn in distilled water showing the three-layered embryophore (MHNG-PLAT-82172); additional layer marked by an arrow. *Abbreviations*: ao – apical organ; cg – cells with finely granular cytoplasm; ci – cirrus; cs – cirrus-sac; do – dorsal osmoregulatory canal; em



– embryophore; lm – internal longitudinal musculature; mg – Mehlis glands; nl – longitudinal nerve; oe – outer envelope; on – oncospheres; ov – ovary; sc – subtegumental cells; so – small outgrowths; te – testes; ud – uterine diverticles; ut – uterus; va – vas deferens; vc – vaginal canal; vd – vitelloduct; vi – vitelline follicles; vo – ventral osmoregulatory canals; vs – vaginal sphincter. Scale-bars: 8 = 100 µm; 9 = 250 µm; 10–11 = 500 µm; 12 = 50 µm.

Vitelline follicles medullary, arranged in two lateral fields near margins of proglottides, occupying 90-95% of proglottis length, interrupted at level of cirrus-sac (Figs 13, 14).

Vaginal canal forming small seminal receptacle anterodorsal to ovarian isthmus. Terminal part of vaginal canal (pars copulathrix vaginae) surrounded by large vaginal sphincter and chromophilic cells (Fig. 9). Vagina anterior (62%; n = 26) or posterior (38%) to cirrus-sac.

Primordium of uterine stem medullary, present in immature proglottides. Development of uterus of type 1 according to de Chambrier *et al.* (2004): in immature proglottides, uterine stem straight, occupying most length of proglottis but never crossing ovarian isthmus, formed by wide longitudinal band of chromophilic cells situated along midline of proglottides. Lumen of uterus appearing in first mature proglottides (Fig. 13); diverticula (lateral branches) formed before first eggs appear in uterine stem. In pregravid proglottides, uterus occupying up to 33% of proglottis width, with 41-68 thin-walled lateral diverticula on each side. In gravid proglottides, diverticula occupying up to 80% of proglottis width. Uteroduct enters uterus almost at level of ovary isthmus.

Eggs round, with outer envelope 140-165 in diameter (Fig. 12). Embryophore spherical, with thick supplementary spherical layer between outer envelope and oncosphere, thus forming three-layered embryophore: internal layer 18-20 (n = 8) in diameter, middle layer 29-33 (n = 7) in diameter; external layer 34-39 (n = 8) in diameter; External layer of embryophore covered by small outgrowths 2.5-4 long; oncosphere spherical, 14-15 in diameter (n = 8), with three pairs of hooks, 8-9 long (Fig. 12). Eggs mature very fast in uterus and ripe eggs (oncospheres with hooklets) are present in the first pregravid proglottides.

TYPE HOST: *Madagascarophis colubrinus* (Schlegel, 1837) (Serpentes, Lamprophiidae).

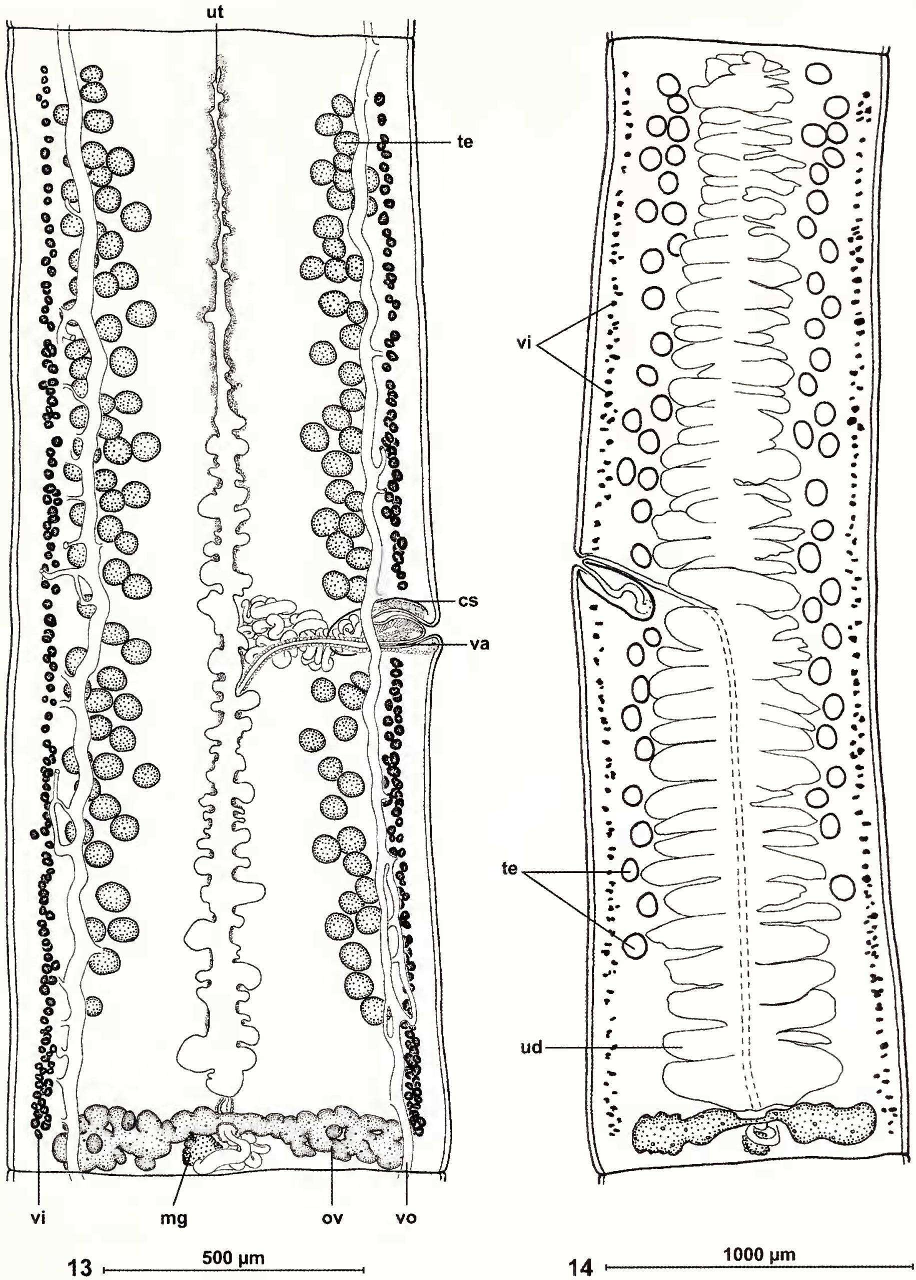
SITE OF INFECTION: Intestine.

PREVALENCE: 2/2 (100%).

ETYMOLOGY: The new species is named after the vernacular local name of the host, i.e. “lapata”.

DIFFERENTIAL DIAGNOSIS: The new species is placed in *Ophiotaenia* La Rue, 1911 (Proteocephalinae) because of the medullary position of the vitelline follicles, the unarmed scolex with uniloculate suckers and testes forming two separate fields (Schmidt, 1986). Ninety-six species of *Ophiotaenia* parasitizing reptiles and amphibians are currently recognized as valid (Freze, 1965; Schmidt, 1986; Ammann & de Chambrier, 2008; Marsella & de Chambrier, 2008; Coquille & de Chambrier, 2008; de Chambrier & de Chambrier, 2010; de Chambrier *et al.*, 2010, 2012). Out of these, 64 species are parasites of snakes (Squamata) (see Table 1 in de Chambrier *et al.*, 2010).

According to Freze (1965), the species of *Ophiotaenia* are limited in their distribution to individual continents and/or zoogeographical regions; this assumption has been then supported by other data, like an high degree of isolation determined by the presence of a number of endemic genera such as *Marsypocephalus*, *Sandonella* (both



FIGS 13-14

Ophiotaenia lapata sp. n. (13) Paratype, mature proglottis, ventral view (MHNG-PLAT-79568). (14) Paratype, schematic view of a gravid proglottis, ventral view (UADBA No 50001). *Abbreviations*: cs – cirrus-sac; mg – Mehlis glands; ov – ovary; te – testes; ud – uterine diverticles; ut – uterus; va – vagina; vi – vitelline follicles; vo – ventral osmoregulatory canals. Scale-bars: 13 = 500 µm; 14 = 1000 µm.

Africa), and *Goezeella* (South America) for fish parasites and *Rostellotaenia* (Africa), *Acanthotaenia* (Asia) and *Kapsulotaenia* (Australia, Papua New Guinea) for reptiles parasites (Freze, 1965); furthermore, for species of *Ophiotaenia* from amphibian hosts (de Chambrier *et al.*, 2006) and from reptilian hosts (Ammann & de Chambrier, 2008), a strict specificity (oioxenous sensu Euzet & Combes, 1980) was observed in all species of this genus. For this reason, the new species is separable from 14 *Ophiotaenia* species found in snakes in Africa (for their complete list, see de Chambrier *et al.*, 2010).

Ophiotaenia lapata sp. n. differs from all but one *Ophiotaenia* species parasitic in African snakes by the presence of an apical organ (Table 1), the only African species possessing an apical organ being *O. adiposa* Rudin, 1917 described from *Bitis arietans* from Cameroun. *Ophiotaenia lapata* differs from *O. adiposa* by its lower number of testes (89-170 versus 170-220), position of the genital pore (situated at 43-53% of the proglottis length from the anterior margin, i.e. almost equatorial in *O. lapata*, versus markedly pre-equatorial, i.e. at 20-25% length of the proglottis in *O. adiposa*) and smaller scolex (width 240-280 µm in the former species versus 500-600 µm in *O. adiposa*) (Table 1).

Ophiotaenia lapata n. sp. also differs from all but one *Ophiotaenia* species parasitic in African snakes in the possession of a third layer of the egg embryophore (Fig. 12). This layer is external to the oncosphere, i.e. it forms the internal envelope of the embryophore. The eggs of all African taxa described until now possess only a two-layered embryophore (Beddard, 1913; Rudin, 1917; Fuhrmann, 1924; Sandground, 1928; Hilmy, 1936; Mettrick, 1960, 1963; Southwell & Lake, 1939; Freze, 1965). A similar structure, i.e. an additional layer of the embryophore, was first observed in some other Proteocephalidea tapeworms (see de Chambrier & Vaucher, 1999; de Chambrier, 2006; Coquille & de Chambrier, 2008; Marsella & de Chambrier, 2008; de Chambrier *et al.*, 2010; de Chambrier & de Chambrier, 2010; de Chambrier *et al.*, 2012).

This character is present in a wide range of proteocephalidean genera and geographical areas, such as *Proteocephalus* (*P. hobergi* de Chambrier & Vaucher, 1999) in Paraguay, *Kapsulotaenia* (*K. sandgroundi* Carter, 1943) in Indonesia, *Cairaella* (*C. henrii* Coquille & de Chambrier, 2008) in Ecuador, *Ophiotaenia* (*O. alessandrae* Marsella & de Chambrier, 2008 in Ecuador, *O. gallardi* (Johnston, 1911) in Australia and *O. bungari* de Chambrier, Binh & Scholz, 2012 in Vietnam). This additional layer of the embryophore, even if it seems to be a convergence phenomenon, is considered as a good discriminant character.

The only African species, the embryophore of which is also three-layered as in the eggs of *O. lapata*, is *O. georgievi* de Chambrier, Ammann & Scholz, 2010 described recently from *Leioheterodon geayi* Mocquard. This species differs from *O. lapata*, besides being devoid of an apical organ (see above and Table 1), by the number of uterine branches (23-28 in *O. georgievi* versus 41-68 in *O. lapata*), and by the total length of the strobila (50 mm in *O. georgievi* versus 295 mm in *O. lapata*).

TABLE 1. Species of *Ophiotaeni*a from reptiles in Africa (modified from de Chambrier *et al*., 2010)

Species	Number of testes	RSCS	Position of the genital pore	Position of the vagina	Apical organ	Width of scolex	Total body length (mm)	Uterine branches on each side	Diameter of eggs
O. adiposa	170-220	26%*	20-25%	ant-post	yes	500-600	300-400	40-50	12**
O. congolensis	65	25%	44-47%*	ant-post	?	?	80	15-20	15
O. crotaphopeltis	94-98	14%*	54%*	?	no	160-180	not given	15-18	26
O. elapsoidae	100-125	24%*	50%*	post-ant	no	1000-1100	150	48-55	
O. gabonica	130-170	18-20%	42%*	generally post	no	300-600	> 380	38-46	39
O. georgievi	92-140	19-32%	44-56%	post-ant	no	225-235	50	23-28	31-35
O. meggitti sp. inq.	86-104	33%	50%*	usually ant.	?	not given	> 68	35	25
O. monnigi sp. inq.	80	10-11%	51%*	ant	?	no scolex	50	50-57	30
O. nigricollis	176-210	20-22%	38%*	ant-post	no	300-310	170	16-20	26-33
O. nybelini	67-90	16-20%	47%*	ant-post	no	105	52	25-40	25
O. ophiodex	110-120	22-25%	>50%	ant-post	no	790-1140	210-270	30-42	27-36
O. southwelli	170-230	46-50%*	50-55%*	ant-post	no	1500	90	8 to 12	30
O. theileri	160-310	20-25%	41-50%*	ant-post	no	400	estimated 300	35-40	18**
O. zschokkei	160-200	20-25%	50%	usually ant.	no	400	estimated 550-600		18**
***O. lapata* sp. n.**	89-170	19-25%	43-53%	post-ant	yes	190-280	295	41-68	34-39

Abbreviations: RSCS = relative size of the cirrus-sac expressed as percentage of its length to the width of the proglottis from the anterior margin; * - taken from figures in Freze (1965); ** - diameter of oncosphere.

TABLE 2. Cestodes parasites of reptiles and amphibiens from Madagascar (Coll. Brygoo)

No	Host	Genus	species	locality	Date	Parasites	No MHNG-PLAT-
181/62	R.219	*Chalanodon*	*madagascariensis*	St Augustin	7.1962	*Oochoristica* sp.	73278
197/67	R.632	*Ithycyphus*	sp.	Perinet	2.1968	*Deblocktaenia* sp.	73277
27/68	R.638	*Lioheterodon*	*geayi*	Antananarivo	4.1968	***Ophiotaenia georgievi***	65470 - 65477
207/63	R.290	*Lioheterodon*	*modestus*	Tanandava	11.1962	Cestode	
28/61	R.63	*Lioheterodon*	*modestus*	Ejeda-Betioky	4.1961	*Ophiotaenia* sp. 1	62581
38/69	R.667	*Lioheterodon*	*modestus*	Befandriana	12.1969	*Ophiotaenia* sp. 1	73261
199/61	R.171	*Liopholidophis*	*lateralis*	Tana	11.1961	*Ophiotaenia* sp. 2?	
48/64	R.409	*Liopholidophis*	*sexlineatus*	Andramasina	2.1964	*Ophiotaenia* sp. 2	73260
181/67 a	R.628	*Madagascariophis*	*colubrina*	Befandriana	10.1967	***Ophiotaenia lapata***	73222
181/67 b	R.628	*Madagascariophis*	*colubrina*	Befandriana	10.1967	*Ophiotaenia* sp. 3	73225
183/67	R.629	*Mimophis*	*mahafalensis*	Plateau Mahafaly	10.1967	*Ophiotaenia* sp. 4	73276
299/62	R.242	*Mimophis*	*mahafalensis*	Lac Bemanta	10.1962	*Ophiotaenia* sp. 4	73282
208/63	R.291	*Sanzinia*	*madagascariensis*	Ambavaniasy	4.1963	*Ophiotaenia* sp. 5	73279
71/70		*Anodonthyla*	*montana*	Andringitra	1.1971	*Ophiotaenia* sp. 6	73267
78-70	R.678	*Lioheterodon*	*geayi*	Antananarivo	4.1968	***Ophiotaenia georgievi***	73212
97/65	R.531	*Madagascariophis*	*colubrina*	Befandriana	8.1965	*Ophiotaenia* sp. 3	73274
By 187		*Rana*	*mascareniensis*	Maintirano		*Ophiotaenia* sp. 7	73273

DISCUSSION

Glaw & Vences (1994) and Vences *et al.* (2009) listed about 300 species of reptiles in Madagascar, most of them (92%) being endemic. Up to now, only two proteocephalidean cestodes, *Deblocktaenia ventosaloculata* (Deblock, Rosé & Broussart, 1962), and *Ophiotaenia georgievi* de Chambrier, Ammann & Scholz, 2010, were described from these reptiles (Freze, 1965; de Chambrier *et al.*, 2010). *Ophiotaenia lapata* n. sp. is the third species of proteocephalideans and the second member of *Ophiotaenia* reported from this country. However, it is evident that the richness of cestode fauna of reptiles in Madagascar is poorly known and it is reasonable to expect that it is much higher than indicated by the available data.

Samples of Cestodes from reptiles and amphibians collected by G. Brygoo have been deposited in the Natural History Museum in Geneva. Nine endemic hosts were found to be infected with proteocephalidean cestodes (Table 2). The material collected by G. Brygoo between 1961 and 1970 in Madagascar in reptiles and amphibians is particularly rich. A preliminary evaluation of these specimens has indicated that there are probably as many as seven unnamed species and that each of them occurs in only one host species, thus exhibiting a strict specificity (oioxene type sensu Euzet & Combes, 1981) (see Table 2 and de Chambrier *et al.*, 2010). One host, *Madagascarophis colubrinus*, probably harbours two different cestode species, i.e. *O. lapata* and another species of *Ophiotaenia* (designated as *Ophiotaenia* sp. 3 in Table 2), which bears a huge apical organ.

The taxonomic evaluation has also shown that only few of these seven potentially new *Ophiotaenia* species can be described because they are not well enough preserved to enable a morphological description. In addition, the specimens were fixed with formalin and thus are unsuitable for phylogenetic studies using molecular data. It is thus obvious that new material should be collected in order to better describe the still hidden diversity of reptilian parasites in Madagascar and to elucidate their phylogenetic relationships.

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